

Reduction in Genetic Variability for Quantitative Trait Prescutellar Bristle Number of Melon Fly [*Bactrocera (Zeugodacus) cucurbitae* (Coquillett)]

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Abstract

Cheng, E. Y., Z. H. Wang, Y. B. Huang, M. Y. Chiang, H. Y. Lu, D. H. Wu, C. M. Yang, and C. C. Nien. 2018. Reduction in genetic variability for quantitative trait prescutellar bristle number of melon fly [*Bactrocera (Zeugodacus) cucurbitae* (Coquillett)]. J. Taiwan Agric. Res. 67(4):337–346.

The number of prescutellar bristles (prsc) in melon fly, *Bactrocera (Zeugocacus) cucurbitae* (Coquillett), is quantitative genetic controlled. The polygenic characters are usually expressed in the continuous traits, but the prsc polymorphism in melon flies are limited to only two phenotypes, 2 prsc phenotype (2PHT) and 4 prsc phenotype (4PHT) at 95% and 5% of the field population, respectively. How a single phenotype dominated a complete prsc trait in genetics and this phenotype happen to have the fewest prsc number among all phenotypes, and how the prsc variability is reduced may be the first question to be studied. A multiple prsc (MB) strain with 6 to 19 prsc bristles and operated only on additive quantitative genetics has been chosen to compare the prsc variability of 2PHT. Both 2PHT and 12PHT were separately single paired with 6, 8, 10, and 12 prsc phenotypes in two serial crosses and the prsc phenotypes of their progeny were analyzed for possible clues. In 2PHT serial crosses, the prsc mean (PM) varied from 3.6 to 4.7 in a 4–8 prsc midparent (MP) window, the biological buffering effect replaced the additive variation of quantitative genetics, as the variation of PM is buffered within 1.1 prsc. In MB series, within a MP window of 9–12 prsc, the PM varied additively from 8.5 to 12.0 prsc without prsc number reduction. The buffering and additive effect of prsc with respected to 2PHT and 12PHT serial crosses were illustrated in the PM–MP map (modified from the genotype-phenotype map or G-P map). The comparative study confirmed that 2PHT is the genetic source of prsc variability reduction. By the backcross tests of 2PHT progeny, the heritability and the cumulative effect of prsc reduction were observed. A simulation of random mating between 2PHT and MB strain was conducted, 2PHT and MB strains mated freely and the reproductive advantage was estimated at 3/2 for 2PHT, another possible factor in reducing the prsc number and variability. Once MB strain mated with 2PHT, the prsc variability reduction could be functional in stabilizing selection for generations, as the observation of four generations of sibling mating, the PM lowered from 4.9 to 3.2, the variance lowered from 15.0 to 2.7, and prsc phenotype trait shortened from 19 to 11 bristles.

Key words: Quantitative genetic, Prescutellar bristle, Melon fly.

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INTRODUCTION

In *Drosophila*, the scute mutant, a fly that lacked a few large bristles (macrochaetes) has been started serial studies of different alleles removed different subsets of bristles, and the investigation led to the important finding of achaete-scute gene complex (AS-C). The molecular dissection of AS-C provides support to the claim that scute can be subdivided into several smaller regions, each is responsible for the development of one or a few macrochaetes (Ghysen & Dambly-Chaudière 1988). Another important feature of bristle development is the generation of species-specific two-dimensional patterns. On each half of the dorsal mesothorax of *Drosophila melanogaster*, 11 macrochaetes occupy precisely constant positions (Lindsley & Zimm 1992). The evolution of bristle number and patterns in Diptera were extensively compared and proposed that all species display four rows macrochaetes on mesothorax as they are acrostichal (AC), dorsocentral (DC), intra-alar (IA), and supra-alar (SA) bristles (Simpson *et al.* 1999; Simpson & Marcellini 2006). In the Acalyptrata, there is usually only a single postsutural AC bristle, called the prescutellar (Simpson *et al.* 1999). The prescutellar belonged to the achaete sets of bristles in *Drosophila* (García-Bellido 1979), and regulated by T5 gene on the AS-C chromosome segment in the molecular and phenotypic map (Ghysen & Dambly-Chaudière 1988). The melon fly, *Bactrocera (Zeugodacus) cucurbitae* (Coquillett), is recorded with 2 prescutellar bristles (prsc) (White & Elson-Harris 1992), and some 4 prsc specimens are collected in the fruit fly control project, since fruit fly is the international quarantine pest, any new, unidentified or invaded species will impose severe threat on fruit production and trade. It becomes necessary to clarify whether there is another pest species or just the prsc polymorphic variant of melon fly. The laboratory study confirmed that 2 prsc phenotype (2PHT) and 4 prsc phenotype (4PHT) interbreed normally. The study of prsc polymorphism started in 1994 with the ques-

tion of why a small portion of individuals with 4PHT exists in a wild population with most of individuals exhibiting 2PHT. After concluding the prsc is quantitative genetic controlled (Cheng *et al.* 2014), the same question takes a turn; as why a single 2PHT phenotype dominates a continuous prsc trait, which contradicts to the principle of quantitative genetics (Emerson & East 1913). The domination of the 2PHT does not come without a reason. However, very little is known about the function of notal bristles; and therefore, it is difficult to speculate on the nature of such selective pressures (Simpson *et al.* 1999) and the variability of polygenic prsc of MB strain must be genetically reduced to only two phenotypes. The 2PHT surge (Cheng *et al.* 2018) in the wild strain can contribute 22% increase in the second filial (F_2) generation and it is not enough to explain the 2PHT domination. The most discussed wild type robustness concept in quantitative genetics is the epigenetic canalization theory proposed by Waddington (1942, 1947). The canalization concept in population genetics has been illustrated more detail by Ridley (2011) as “canalized relation” and Hansen (2006) related the genotype-phenotype map to canalization. The non-linear relationship between genotype and phenotype produced remarkable response to selection. Particularly on the variability reduction, Gibson & Wagner (2000) defined the biological systems evolve to a state of higher stability against mutational and environmental perturbations, through the reduction in variability of a trait. In this study, the prsc variability was examined by crossing the wild type to other selected strains for the evidence of 2PHT robustness.

MATERIALS AND METHODS

Insect materials

The insect rearing, selection and the definition of bristles (White & Elson-Harris 1992; Drew & Hancock 1994) were the same as described in the previous report (Cheng *et al.*

2014).

- (1) The 2 prsc (2P) phenotype strain was selected from the laboratory reared wild strain (Cheng *et al.* 2014), the prsc mean = 2.0 ± 0.17 , and the prsc traits = 1–4.
- (2) The multiple prscs (MB) strain was selected from a laboratory reared 4PHT strain (Cheng *et al.* 2014), the prsc mean = 12.3 ± 1.9 , and the prsc traits = 6–19.

The prsc variability test

The prsc genetic variability was investigated in 2P and MB strains serial crosses, the prsc mean (PM), the prsc midparent (MP) values (Ridley 2011) and the prsc trait variances of F_1 and F_2 progeny were compared. The units for PM and MP are prsc bristles. The virgin 2PHT individual of 2P strain was single paired with the opposed-sex virgin individual of 6, 8, 10, and 12PHT (from MB strain), while the virgin 12PHT individual was single paired with the oppose-sex virgin individual of 6, 8, 10, and 12PHT (all from MB strain). Each pairing test has 4–6 replicates, and the F_1 progeny was sibling mated to the F_2 generation for the prsc phenotype frequency distribution (PFD) analysis. The PM correlated to MP is illustrated in the PM–MP map (modified from the genotype–phenotype map, G–P map, Hansen 2006).

The cumulative effect of prsc variability changes

The F_1 sibling of $2P \times MB$ cross was backcrossed to 2P and MB strains to examine the heritability of the prsc number variation. The resulted phenotypic traits were analyzed for the PM reduction from expected MP (Conner & Hartl 2004). PM reduction = $100\% \times 2 \times (MP - PM)/(HPN - LPN)$, HPN and LPN are high and low parental prsc numbers in a cross.

The reproductive advantages between 2P and MB strains

The MB strain is essentially absented in the field population, and it is interesting to know whether the wild type (2P strain) has

any reproductive advantage over MB strain. To simulate the field condition, a sub-population of 80 flies was created by grouping 20 virgin males, 20 virgin females from both 2P and MB strains in one cage to allow random mating occur, and the experiment was done in three replicates. The component analysis of prsc trait is possible, because the prsc traits of 2P and MB strains were completely independent from each other, while 94% prsc trait of F_1 progeny were independent with only 2.5% and 3.5% overlapping with respect to 2P and MB traits. In analysis, the overlapped phenotype frequencies were distributed by the peak height ratio to three trait standards.

Trend study of prsc variation

The F_1 offsprings of the random mating were sibling mated for three more generations, and their prsc PFDs were traced for variation.

RESULTS

The prsc variability was reduced by 2P strain

In 2P serial crosses, the PM of both F_1 and F_2 progeny were suppressed below 5 prsc, and lower than expected MP. The 2×12 cross for example, the PM = 4.7 reduced 46% from expected MP of 7.0 for both F_1 and F_2 progeny (Table 1 & Fig. 1A). In a 4–7 prsc MP window, the PM merely varied 1.1 prsc from 3.6 to 4.7 prsc and 3.5 to 4.7 prsc in F_1 and F_2 progeny, respectively (Table 1). The variability reduction or the biological buffering of prsc is illustrated in the PM–MP map (Fig. 2A). In MB serial crosses, the PM remained equally to MP in a 9–12 prsc window (Table 2), and followed the additive variation of quantitative genetics. The PM–MP map shows no sign of biological buffering (Fig. 2B). The variances of F_1 progeny in 2P series remained consistently at 1.0 (Table 1) and indifferent to the MP change. The variances of F_2 progeny increased with the MP (Table 1), but the 2PHT surge (Cheng *et al.* 2018) disturbed the continuous trait and

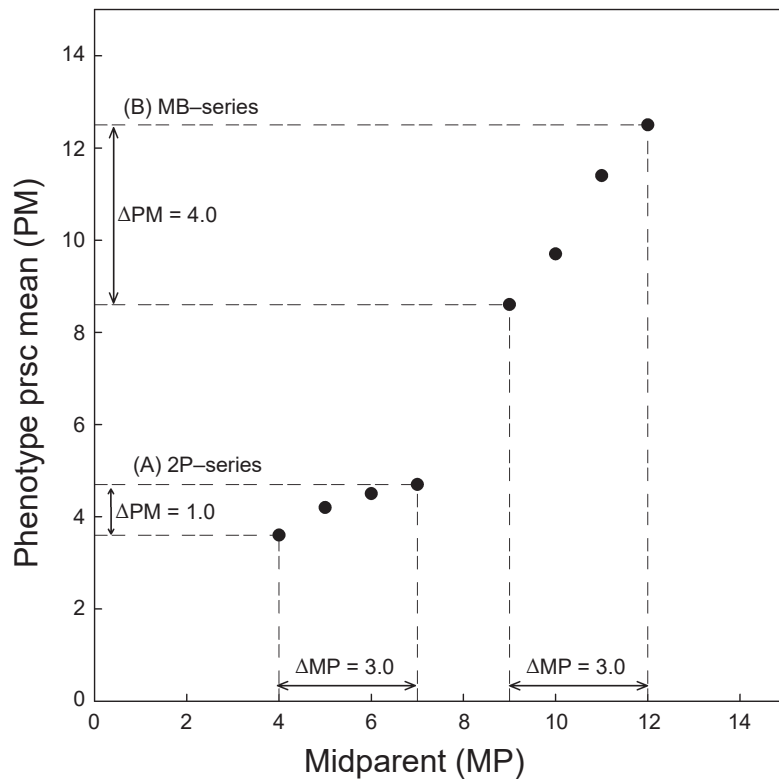


Fig. 2. The prescutellar bristles (prsc) mean (PM)–midparent (MP) map of 2 prsc (2P)– and multiple prsc (MB)–serial crosses. The mapping from MP to PM is a mathematical function that assigns a phenotypic change to each change in MP. (A) In 2P–series, the flat region a given MP change (ΔMP) has a small effect (ΔPM), whereas the same MP change in the steep region of the (B) MB–series has a large effect. Canalization is evolution toward flat regions, whereas decanalization is evolution toward steep regions (Hansen 2006).

Table 2. The mean, variances, and midparent value of prescutellar bristles (prsc) in F_1 and F_2 progeny of the multiple prsc (MB) strain crosses.

Parent's phenotype	MP ^z	F ₁		F ₂	
		PM ^y	Var. ^x	PM	Var.
12 × 6	9.0	8.5 (581) ^w	4.0	8.7 (992)	3.7
12 × 8	10.0	10.2 (601)	4.6	9.2 (783)	5.0
12 × 10	11.0	11.5 (220)	4.4	11.3 (946)	4.9
12 × 12	12.0	12.3 (3,338)	5.2	12.6 (3,872)	5.8

^z MP: midparent value.

^y PM: prsc mean.

^x Var.: variance of phenotype frequency distribution.

^w Sample size.

The prsc number reduction by 2P strain is cumulative and heritable

The 2P strain has been identified as the source of prsc variability reduction. In order

to understand whether this reduction ability is heritable or not, the F_1 progeny of $2P \times MB$ (Fig. 1A) was backcrossed to both 2P and MB strains. In $2P \times (2P \times MB)$ backcross (Fig. 1B), half the F_2 progeny were affected by

2PHT surge (Cheng *et al.* 2018), and after the correction, the MP was expected at 3.4. The PM of the backcross progeny was 3.0, a 30% reduction from the MP. The result indicated the prsc number reduction could be accumulated in repeated crosses of 2P strain. In MB \times (2P \times MB) backcross (Fig. 1C), the resulted PM was 6.1, a 66% reduction from the MP of 8.5. This second backcross confirmed the F₁ progeny still had the ability in reducing the prsc numbers. When contrasted to a comparable 12 \times 6 cross in MB series (Fig. 1D), the progeny PM was 8.5, merely a 17% reduction from the MP of 9.0. The biological buffering effect continued in generations of 2P progeny, but not in a comparable cross of MB strain, suggesting that the genetic origin of prsc number reduction was related to the 2P strain and heritable.

The reproductive advantage of 2P strain in random mating with MB strain

In the grouping test, 2P \times 2P, 2P \times MB, and MB \times MB are three possible combinations in random mating; each combination produces a unique progeny prsc trait with less than 2.5–3.5% overlapping (Fig. 3A). If the reproductive potential and the mating preference are equal, the probabilities of 2P individual to mate either 2P or MB opposed-sex individual were equal at 50%, and ideally, three components would be 25% : 50% : 25% or 1 : 2 : 1 for 2P, F₁, and MB traits, respectively (Russell 2005; Griffiths *et al.* 2008). The three distinct prsc phenotypic traits of random mating corresponded to 2P, MB, and F₁ trait standards, the overlapped areas were distributed according

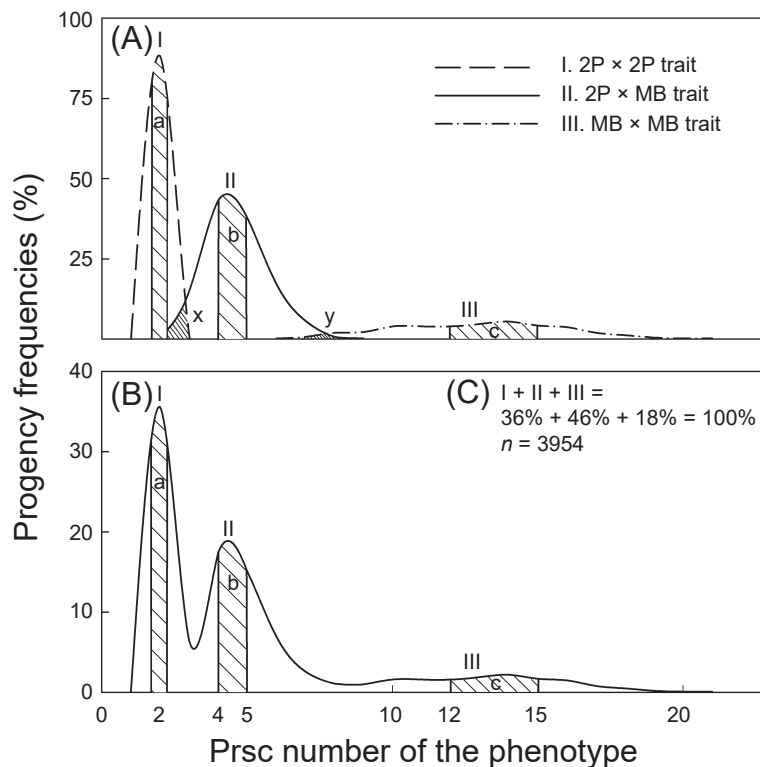


Fig. 3. The component analysis of progeny prescutellar bristles (prsc) traits in the grouping of 2 prsc (2P) and multiple prsc (MB) strains for random mating. (A) Three component traits with 2.5% overlapping (x) between (I) and (II) and 3.5% overlapping (y) between (II) and (III); (B) The overlapping was resolved by ratios between the peak areas (a, b & c, shade areas) to their own standards, a = 2PHT; b = 4–5PHT; c = 12–15PHT; and (C) The resulted progeny prsc traits and their component frequencies.

the peak ratio to their standards (Fig. 3B). The progeny frequencies were 36, 46 and 18% for 2P × 2P, 2P × MB and MB × MB mating combinations, respectively. The reproductive chances were 60% for the 2P individuals and 40% for the MB individuals, instead of expected 50%. The biological advantage of 2P strain is estimated at 3/2 over the MB strain.

The progeny of the grouping test

There were sibling mated for three more generations the PM reduced from 4.9 to 3.2, the variance lowered from 15.0 to 2.7, while the PFD range shortened from 2–19 to 2–11

(Fig. 4). The trend of prsc number reduction continued in these generations and the traits of MB strain gradually been eliminated as that in the field population.

DISCUSSION

In melon fly, the polygenic nature of prsc is contradictory to its “two phenotypes” expression in field population. How the continuous prsc trait reduced to two phenotypes is interesting to know. The paradox was only partially explained by a “2PHT surge” study (Cheng *et al.* 2018), because the inbreeding of F_1 is rare

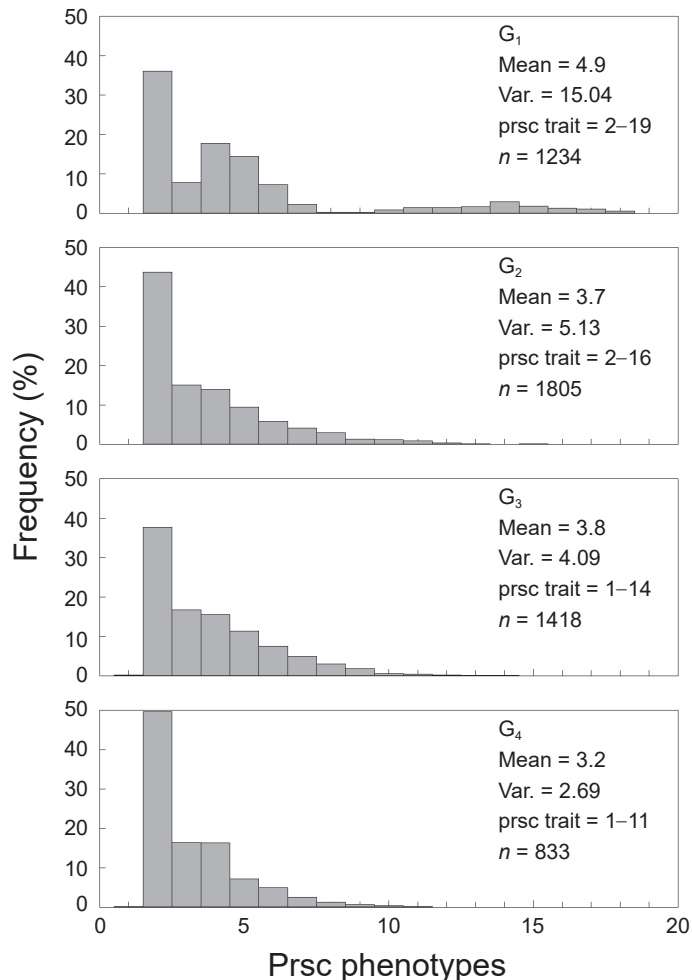


Fig. 4. The progeny prescutellar bristles (prsc) trait analysis in the grouping of 2 prsc (2P) and multiple prsc (MB) strains random mating for four generations.

in field, and the real reason for the wild type robustness is remain to be investigated. The robustness of 2P strain has been explored by comparing to a polygenic MB strain to show that 2P strain has the ability to suppress and buffer the prsc number in either single cross or multiple generations, and the reduction can be calculated (Conner & Hartl 2004).

The prsc variability reduction in this study corresponded to the definition of canalization of reduced trait variability and biological buffering (Waddington 1942; Gibson & Wagner 2000), so as the claim that the stabilizing selection will favor the wild type (Scharloo 1991). There is no previous report on the prsc genetics in melon fly, but the bristle number canalization has been recognized in *D. melanogaster* and related to chromosome 1 and/or 2 (canalizer) while chromosome 3 is responsible for the chaetogen, the embryonic cell to be developed into a bristle is increasing (Garcia-Vazquez & Rubio 1988). Wilkins (1986, 2002) stated that the canalization is by multiple genetic factors within the genome, a form of genetic buffering. The biological polymorphism provides subjects and materials for the trait variability study. Gibson & Hogness (1996) is able to show that canalization of the bithorax phenotype in *Drosophila* was largely caused by the polymorphism in the homeotic gene *Ultrabithorax* (*Ubx*).

This study observed two genetic modifications in prsc traits: (1) the 2P strain is capable in reducing the progeny's prsc number in cross with other phenotypes, and (2) the prsc variability reduction can be inherited and accumulated in following generations to continue the stabilizing selection. Both modifications contributed to the robustness of 2PHT and its domination in the field population as Slarkin (1985) indicated that the gene flow favoring the wild type to be continued and intensified for generations. Whether the prsc variability reduction fits the theoretical speculation of canalization (Wagner *et al.* 1997), in particular, the canalization proceeds in multiple

generations or only in the embryo development remains to be discussed. Without the variability reduction, the prsc number in MB strain followed the additive variation of quantitative genetics accordingly. Since the MB strain has not been found in the field population and the Hardy-Weinberg equilibrium (Ridley 2011) between 2P and MB strains can never be an issue to be discussed. The reproductive advantage of 2P strain might be another factor in reducing or eliminating the MB traits in field population.

CONCLUSIONS

The prescutellar bristles of melon fly can be another polymorphism model, as *D. melanogaster*, to study the variability of quantitative traits. This prsc study began with a simple question of what is the prsc polymorphism in melon fly. First thing find out was the quantitative genetics of prsc, then came the genetic interaction of "2PHT surge" in a quantitative trait. The prsc variability reduction expended our view in wild type robustness and canalization. Now we know that the simple question asked in 1994 was not that simple. The genetics of prsc in melon fly is based on the quantitative genetics as the MB strain does; however, the 2P strain dominates the field population because it possess following characteristics in extra: (1) The 2P strain can reduce the prsc variability of MB strain in numbers as well as phenotypes. (2) The prsc variability reduction is heritable and cumulative, and maintains stabilizing selection in generations. (3) The reproductive advantage of 2P strain may also contribute the elimination of MB trait in field population.

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瓜實蠅 [*Bactrocera (Zeugodacus) cucurbitae* (Coquillett)] 中 胸背板剛毛遺傳變異之縮減

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摘要

鄭允、王志賢、黃毓斌、江明耀、呂秀英、吳東鴻、楊崇民、粘君琪。2018。瓜實蠅 [*Bactrocera (Zeugodacus) cucurbitae* (Coquillett)] 中胸背板剛毛遺傳變異之縮減。台灣農業研究 67(4):337–346。

瓜實蠅 [*Bactrocera (Zeugodacus) cucurbitae* (Coquillett)] 之中胸背板剛毛 (prescutellar bristles; prsc) 係由數量遺傳 (quantitative genetics) 控制，其數量由 2–20 根不等，但野生族群中，2 根剛毛之表現型 (2 prsc phenotype; 2PHT) 卻占 95%，而偏離了連續分布 (continuous trait) 之基本分布，其原因究竟為何？本研究是以 2 prsc (2P) 品系與多剛毛品系 (multiple prsc strain; MB-strain) 進行雜交並觀察其子代之表現型分布頻度進行分析，觀察結果發現 2P 品系 (野生型) 為親本時，壓縮多剛毛品系之表現而偏離數量遺傳之均值原則 (additive)，在二者之子代中，親本之均值 (midparent; MP) 變化為 4–8 prsc 間時，子代 prsc mean (PM) 值為 3.6–4.7 其範圍僅為 1.1，有明顯的緩衝現象 (biological buffering)，可在 MP/PM 圖示中顯示 (比照 genotype–phenotype map, Hansen 2006)。多剛毛品系不同表現型之子代 prsc 則與親本之平均值成正比。MP 在 9–12 prsc 間，PM 之變異也為 9–12 prsc，而依數量遺傳之 additive 準則互動。依 Conner & Hartl (2004) 報導，就 PM 偏離均質 (MP) 方法分析，發現 2P 品系後代之 PM 均低於 MP，在二則回交測試中均顯示 2P 品系之 PM 壓縮特質為可遺傳性，在後繼之子代中且有累進壓縮 prsc 之效應。而在模擬 2P 及 MB 兩品系，在田間以群體方式進行自由選擇繁殖 (random mating) 所產生之子代表現型頻度，發現 2P 品系對 MB 品系有 3:2 之繁殖優勢，而其後續繁殖之子代中，中胸剛毛之平均數量及分布均不斷地減縮，與觀察田間族群之低變異性所得相符。由此研究所得結論為 2P 品系有減少子代 prsc 數量之特質，此特質有遺傳性及累進性。只要與 2P 品系雜交後，prsc 數量即不斷地減少，而趨向田間所見之 2P 野生型。

關鍵詞：數量遺傳、中胸背板剛毛、瓜實蠅。

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